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Laboratory observations on the food preference of *Onychiurus armatus* (Tullb.) Gisin (Collembola, Family Onychiuridae)

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INTRODUCTION

Collembola constitute a numerically important component of the fauna in most soils. The specific contribution of these organisms to soil processes is however, unclear. Collembola may be of importance in humus formation (KUBIENA, 1955), and no doubt take part in decomposition processes through the trituration of organic matter, and the dissemination of fungi (POOLE 1959) and bacteria (TÖRNE 1976 b). However, until food utilisation by Collembola species is enunciated their contribution to soil processes will remain speculative.

A number of studies relating to the food of Collembola are available e.g. MACNAMARA (1924), STEBEL (1932), SCHALLER (1950), POOLE (1959), KNIGHT and ANGEL (1967), TÖRNE (1967 a, b), SINGH (1969), GILMORE and RAFFENSPERGER (1970), BÖDVARSSON (1970), McMILLAN and HEALEY (1971), ANDERSON and HEALEY (1972), McMILLAN (1975). In their natural habitat most soil and litter inhabiting Collembola appear to feed upon decayed and undecayed plant material, fungi, and bacteria, and food preferences are evident. In laboratory culture, results of the few available feeding studies with soil and litter inhabiting Collembola are inconclusive.

McMILLAN (1975), in a study of seasonal and interspecific variations in the gut content of three species of the family Onychiuridae [*Onychiurus armatus* (Tullb.) Gisin, *O. furcifer* (Börner to Gisin, and *Tullbergia callypygos*

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(Börner)] found plant, fungal and mineral material to be the major gut components. Consequently the present study which describes laboratory experiments investigating fungal feeding habits of *Onychiurus armatus* (Tullb.) Gisin, was undertaken.

MATERIALS AND METHODS

1. Foods — Fungi and yeasts.

Fungal species used were chosen because of their predominance in soil and litter in beech (*Fagus sylvatica* L.) woodland (CALDWELL, 1963; JENSEN, 1963 a, b, 1964; HOGG and HUDSON, 1966); a habitat similar to that in which studies of the biology of a population of *Onychiurus armatus* were made (MCMILLAN, 1975). Fourteen species of fungi and 18 species of yeasts were used (Table I). All species were cultured and maintained on 2 % Malt Extract Agar. Fungi were supplied by the Commonwealth Mycological Institute, Surrey, England, and by Dr M. J. SWIFT, Birkbeck College, University of London, England. Yeasts were supplied by the Curator, National Collection of Yeast Cultures (The Brewing Industry Research Foundation, Surrey, England) and by Dr J. H. BAKER, Freshwater Biological Association, Dorset, England.

2. Animals.

Individuals of *Onychiurus armatus* were collected as required from soil taken from the periphery of a nest of *Formica rufa* L (woodland ant). The nest was located in a mixed coppice of beech and sweet chestnut in Blean Woods National Nature Reserve, near Canterbury, in south-east England. Collembola were collected alive, after their extraction from soil using a Tullgren type funnel. Animals were confined without food in sterilised pyrex culture chambers, containing a plaster of Paris and charcoal mixture substrate (GOTO, 1961) for up to 12 hours prior to experiments. A relative humidity of 90-100 % was maintained within the culture chambers by moistening the substrate with a few drops of sterilised distilled water. Culture chambers were maintained at 15° ± 1° C. Only active and apparently healthy individuals, representing a range of ages, were used as experimental animals.

3. Feeding experiments.

Feeding experiments were conducted in covered, sterilised, petri dishes, 150 mm. and 50 mm diameter, containing a plaster of Paris and charcoal mixture substrate (GOTO, 1961), and with a relative humidity of 90-100 %.

Food samples consisted of discs of fungi 5 mm in diameter, with as much agar as practicable removed, and slabs of yeast 4 × 4 × 1 mm. Samples of fungi and/or yeasts were introduced into the petri dishes 12 hours before the animals. Two replicates of each food were laid out on the freshly moistened substrate surface at random, but within the confines of a superimposed grid, as follows:

(i) each food lay no less than 10 mm from its nearest neighbours.

(ii) no two replicates were nearest neighbours.

(iii) no food lay closer than 10 mm to the petri dish wall.

Animals were released into a clear area 20 mm in diameter in the centre of the petri dishes. One hundred animals, and 20 animals were used for experi-

TABLE I

Foods presented to *Onychiurus armatus* (Tullb.)

FUNGI	Food Code
Fam. Mucoraceae	
Absidia spinosa Lendner	F. C
Mucor ramannianus Moeller	F. I
Fam. Moniliaceae	
Aspergillus niger van Tieghem	F. J
Penicillium nigricans Bainier	F. B
Penicillium chrysogenum Thom	F. G
Gliocladium roseum (Link) Thom	F. A
Botrytis cinerea Persoon	F. L
Trichoderma viride Persoon	F. N
Fam. Dematiaceae	
Pullularia pullulans (de Bary) Berkhout	F. E
Cladosporium herbarum (Persoon) Link	F. K.
Alternaria tenuis Nees	F. M
Fam. Tuberculariaceae	
Epicoccum nigrum Link	F. H
Fam. Agaricaceae	
Collybia peronata Bolt	F. D
Mycena galopus (Pers.) Fr	F. F
YEASTS	
Fam. Saccharomycetaceae	
Saccharomyces fructuum Lodder et Kreger-van Rij	Y. F
Lipomyces starkeyi Lodder et Kreger-van Rij	Y. L
Fam. Cryptococcaceae	
Cryptococcus albidus (Saito) Skinner strain ' A '	Y. I
C. albidus strain ' B '	Y. H
C. albidus strain ' C '	Y. R
C. laurentii (Kuff.) Skinner	Y. M
Candida curvata Diddens et Lodder	Y. K
C. humicola (Daszewska) Diddens et Lodder	Y. O
C. krusei (Cast.) Berkh	Y. J
C. solani Lodder et Kreger-van Rij	Y. B
Torulopsis candida (Saito) Lodder	Y. P
T. famata (Harrison) Lodder et Kreger-van Rij	Y. G
T. ingeniosa di Menna	Y. D
Trichosporon capitatum Diddens et Lodder	Y. C
T. cutaneum (de Beurm., Gougerot et Vaucher) Ota	Y. N
Schizoblastosporion starkeyi-henricii Ciferri	Y. A
Fam. Rhodotorulaceae	
Rhodotorula rubra (Demme) Lodder	Y. E
R. mucilaginosa (Jörg.) Harrison	Y. Q
Malt Extract Agar (2 % w/v)	MEA

ments conducted in large (150 mm) and small (50 mm) petri dishes respectively. Small petri dishes were used in experiments with up to three species of fungi or yeasts, whereas large petri dishes were used when more species were being tested.

Experiments were usually run for 60 hours, with the feeding activities of animals noted via a dissecting microscope at hourly intervals during the first, third, and fifth, 12 hour periods. Animals designated as feeding were those Collembola which appeared to be actively ingesting fungus or yeast. Animals were released into petri dishes one hour prior to the first recorded observation. Experiments were run at 15° ± 1° C, and in the dark, except during hourly inspection when they were exposed to red light. Three replicates of dishes were used for each experiment.

4. Design of experiments.

a) *The movement of marked Collembola between foods.*

The movement of individuals between foods within a petri dish is likely to influence food selection. Therefore, to determine movements of Collembola, a number of individuals were marked with spots of different coloured paints, ten marked and 90 unmarked Collembola were released into a large petri dish containing discs of 14 species of fungi. The positions of marked individuals were recorded hourly during the first, third, and fifth 12 hours of a 60 hour period. Three replicate experiments were conducted. Analogous experiments were conducted using 18 species of yeasts.

The substance used to mark the non-wettable cuticle of *O. armatus* was a cosmetic lipstick, suspended in boiled linseed oil. Individuals marked with lipstick preparation showed no obvious ill effects, and the marked skin was shed during the animal's next ecdysis.

b) *Feeding preference.*

Multi-choice experiments using either species of fungi or yeasts were conducted to determine food preferences. The experiments were as follows:

(i) Three fungi, or three yeasts were presented

(ii) all fungi, or all yeasts were presented

(iii) all fungi, or all yeasts were presented, and prior to the last 12 hours of observations the positions of foods were interchanged. A more preferred food was interchanged with a less preferred food.

(iv) A mixed selection of fungi and yeasts, comprising the more preferred species, as determined from experiments (i), (ii), (iii) above were presented.

Addition experiments were conducted with fungi to determine if *O. armatus* were selective for hyphae or spores.

Experiments with cultures containing hyphae with spores. Three samples, each containing hyphae and spores of a single species were placed in a small petri dish, together with 10 *O. armatus* with visibly empty guts. At intervals of 12 and 36 hours two Collembola with visibly full guts were removed. The animals were asphyxiated and mounted in A. C. S., an insect mounting medium (Searle Laboratoires, Buskinghamshire, England), between slide and coverslip and the numbers of spores and hyphae counted.

Experiments with cultures containing hyphae without spores, and hyphae

with spores. The two fungi used in this study, *Trichoderma viride* and *Botrytis cinerea* are prevented from sporulation when grown exposed to red light. Samples of *T. viride*, or *B. cinerea* containing hyphae alone, and hyphae with spores, were placed in small petri dishes together with 20 *O. armatus*. The feeding preference of individuals was noted hourly during the first and third 12 hours of a 36 hour period.

RESULTS

a) Movement of Collembola between foods.

Two typical examples of the charted movement of a marked Collembola, one, between fungus foods and the other, between yeast foods, noted hourly during the first, third, and fifth 12 hours, of a 60 hour period are shown in Figure 1, I and II. These clearly show that the Collembola moved extensively about the substate surface of petri dishes, and sampled more than one food. Individuals were recorded on the same food disc, apparently ingesting fungus or yeast, for a maximum of six and eight successive hourly observations respectively.

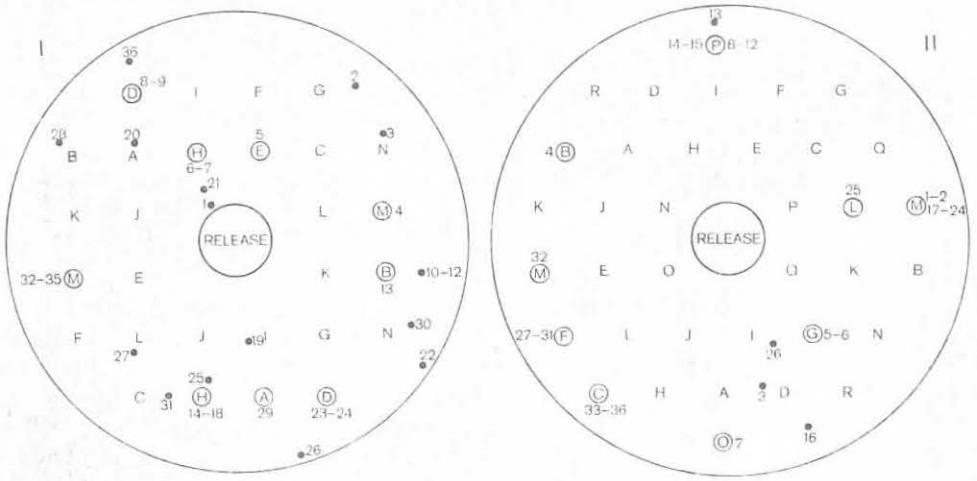

FIG. 1. — The charted movement of one *Onychiurus armatus* (Tullb.) between fungal foods during 36 hours.

I : between fungus foods (A-N, see food code number, Table 1).
II : between yeast foods (A-Q see food code number Table 1).
Key : 1-36, designates hours; ◯, designates animal feeding on food; ● designates position of animal, not feeding.

b) Food preference.

The significance of food preferences exhibited by *O. armatus* were tested by chi-square analysis on hourly data, 12 hours data, and total data in each experiment (as the food preferences obtained from three sets of data per

experiment were similar, only one set of data are given). Howeved, as individual Collembola were observed to remain on the same fungus, or yeast, for up to six and eight successive observations, the determined chi-square may be invalid. Therefore, the appropriate results of chi-square are also divided by six for fungus, by eight for yeast, or by seven for the mixed fungus/yeast experiments.

The results of food preference experiments (Tables II - VI) show that although all foods were apparently ingested by some individuals, *O. armatus* exhibits significant ($P < 0.001$ and $P < 0.05$) differences in its preference for the various foods. Interchanging more favoured foods with those less favoured shows that food position was not related to food preference. The total data suggests that most preferred yeasts were:

Candida curvata, Cryptococcus laurentii, Saccharomyces fructum,

Schizoblastosporion starkeyi-henricii, Torulopsis candida, and *T. famata. Least preferred yeasts were:*

Cryptococcus albidus strain 'A', *C. albidus strain* 'B', *C. albidus* strain 'C' *Rhodotorula mucilaginosa, R. rubra, Torulopsis ingeniosa,* and *Trichosporon cutaneum.*

TABLE II

Onychiurus armatus **(Tullb.) yeast preference experiments and χ^2 analysis**

(a) Choice of 3 species. Total data; 2,12 hourly periods as 1×3 contingency tables.

Yeasts [+]	YA	YB	YC	YD	YE	YF	YG	YH	YI	YJ	YK	YL	YM	YN	YO	YP	YQ	YR
Animal totals	197	160	224	45	56	417	504	9	61	204	271	196	410	60	238	458	6	81
χ^2 (3 d.f.)	10.64*			518.15***			774.17***			15.19***			258.70***			645.92***		
$\chi^2/8$ (3 d.f.)	1.33 n.s.			64.77***			96.77***			1.90 n.s.			32.34***			80.74***		

(b) Choice of 18 species. Total data; 3,12 hourly periods as 1×18 contingency table.

Yeasts [+]	YA	YB	YC	YD	YE	YF	YG	YH	YI	YJ	YK	YL	YM	YN	YO	YP	YQ	YR
Animal totals	696	354	174	39	41	555	1095	32	26	396	468	299	562	27	278	376	7	8
χ^2 (18 d.f.)	5017.32***																	
$\chi^2/8$ (18 d.f.)	627.16***																	

(c) Choice of 18 species. Positions of yeasts interchanged. Data 3,12 hourly periods as 3×18 contingency table.

Yeasts [+]	YA	YB	YC	YD	YE	YF	YG	YH	YI	YJ	YK	YL	YM	YN	YO	YP	YQ	YR
0-12 hour animal totals	225	55	64	17	96	230	462	8	20	274	220	94	134	53	121	434	1	2
24-36 hour animal totals	149	101	78	5	69	297	708	3	1	268	179	74	152	10	209	210	0	0
Yeasts [+] interchanged [++]	YQ	YL	YF	YJ	YO	YC	YI	YK	YG	YD	YH	YB	YR	YP	YE	YN	YA	YM
48-60 hour animal totals	2	82	109	49	93	72	13	104	155	11	11	55	11	85	10	51	100	281
χ^2 (34 d.f.)	1338.92***																	
$\chi^2/8$ (34 d.f.)	542.37***																	

Significance *** $P < 0.001$
* $P < 0.05$
n.s. not significant
d.f. degrees of freedom
\+ see Table I
++ YA interchanged with YQ etc.

TABLE III

Onychiurus armatus **(Tullb.) fungus preference experiments and χ^2 analysis**

(a) Choice of 3 species. Total data; 2,12 hourly periods as 1×3 contingency tables.

Fungi+	FA	FB	FD	FC	FN	FM	FE	FF	FL	FG	FH	FK	FI	FJ	FA
Animal totals	534	32	49	310	42	332	91	47	272	454	102	233	509	13	377
χ^2 (3 d.f.)	793.64***			228.51***			208.93***			240.71***			439.71***		
$\chi^2/6$ (3 d.f.)	132.27***			38.08***			34.82***			40.12***			73.29***		

(b) Choice of 14 species plus agar. Total data; 3,12 hourly periods as 1×15 contingency table.

Fungi+	FA	FB	FC	FD	FE	FF	FG	FH	FI	FJ	FK	FL	FM	FN	MEA
Animal totals	206	251	75	613	809	479	303	609	659	587	38	320	146	16	10
χ^2 (15 d.f.)	2827.18***														
$\chi^2/6$ (15 d.f.)	471.20***														

(c) Choice of 14 species plus agar. Positions of fungi interchanged. Data; 2,12 hourly periods as 2×15 contingency table.

Fungi+	FA	FB	FC	FD	FE	FF	FG	FH	FI	FJ	FK	FL	FM	FN	MEA
0-12 hour animal totals	446	13	176	49	49	9	195	83	457	50	123	71	103	59	1
Fungi+ interchanged++	FJ	FG	FN	FH	FK	FI	FB	FD	FF	FA	FE	FM	FL	FC	MEA
24-36 hour animal totals	28	216	50	42	161	587	28	15	74	406	25	282	22	121	1
χ^2 (14 d.f.)	2230.92***														
$\chi^2/6$ (14 d.f.)	371.82***														

Significance *** $P < 0.001$
d.f. Degrees of freedom
\+ See Table I
++ FA interchanged with FJ etc.

TABLE IV

***Onychiurus armatus* (Tullb.) yeast/fungus preference experiments and χ^2 analysis. Choice of 12 species. Total data ; 3, 12, hourly periods as 1×12 contingency table**

Yeast/fungus+	YG	FM	YJ	FG	FA	YF	FI	YA	FK	YK	YP	FC
Animals totals	70	199	21	41	294	272	376	186	117	80	329	54
χ^2 (12 d.f.)	959.60***											
$\chi^2/7$ (12 d.f.)	137.08***											

Significance *** $P < 0.001$
d.f. Degrees of freedom
\+ See Table I

The most preferred fungi were: *Absidia spinosa, Alternaria tenuis, Botrytis cinerea, Gliocladium roseum, Mucor ramannianus,* and *Penicillium chrysogenum.* Least preferred fungi were: *Penicillium nigricans,* and *Trichoderma viride.* Preference experiments between the more favoured yeasts and fungi (Tabl IV) show two species, the fungus *Mucor ramannianus* and the yeast *Torulopsis candida,* as most favoured by *O. armatus.* Discs of the culture

medium (2 % Malt Extract Agar (MEA)), which contaminated the fungus discs, were included in fungi preference experiments. The medium was however given low preference by *O. armatus*.

All fungus cultures were spore bearing, except the two Basidiomycetes, *Collybia peronata* and *Mycena galopus*. Microscope examination of the gut content of a number of *O. armatus* each of which had previously been confined to one of the sporulating fungi showed that the Collembola ingested more spores than hyphae for eight of the 12 fungi used in this experiment (Table V). There were no obvious differences between gut contents of animals removed from the same culture after intervals of 12 and 36 hours.

TABLE V

Mean (N = 2) percentage of fungal spores and hyphae in the gut of cultured *Onychiurus armatus* (Tullb.)

Fungus	% Spores	% Hyphae
Penicillium chrysogenum	100.0	0.0
Trichoderma viride	99.8	0.2
Gliocladium roseum	99.6	0.4
Aspergillus niger	99.5	0.5
Penicillium nigricans	98.6	1.4
Cladosporium herbarum	98.2	1.8
Mucor ramannianus	94.3	5.7
Pullularia pullulans	82.8	17.2
Alternaria tenuis	16.3	83.7
Epicoccum nigrum	12.1	87.9
Botrytus cinerea	1.9	98.1
Absidia spinosa	0.0	100.0

Results of preference feeding experiments between spores and hyphae of each of the two fungi *Trichoderma viride* and *Botrytus cinerea* show significant differences (Table VI). The sporulating culture of *T. viride* was preferred to the non-sporulating culture, whereas the reverse occured with

TABLE VI

***Onychiurus armatus* (Tullb.) fungus spores/hyphae preference experiments and χ^2 analysis Two species. Total data ; 2, 12, hourly periods as 1 × 2 contingency tables**

Fungi	*Trichoderma viride*		*Botrytus cinerea*	
	Spores	Hyphae	Spores	Hyphae
Animal totals	298	164	351	551
χ^2 (2 d.f.)	40.00***		44.65***	
$\chi^2/6$ (2 d.f.)	6.67*		7.44*	

Significance *** $P < 0.001$
* $P < 0.05$
d.f. Degrees of freedom

B. cinerea. However, sporulating and non-sporulating cultures of each fungus were ingested by *O. armatus.*

DISCUSSION

The present study indicates that under laboratory conditions many species of fungi and yeasts are favourable food for *Onychiurus armatus,* but a few species are significantly more favoured. Evidently some potential foods have characteristics that affect Collembola either favourably or unfavourably.

Studies on the food selection of macrophytophagous insects (e.g. FRAENKEL, 1959; THORSTEINSON, 1960; BECK, 1965; DETHIER, 1966; HSIAO, 1969) indicate that colour, smell and taste are factors which may increase acceptability of food throught stimulation of animal appetite. To the human eye the most and least preferred foods of *O. armatus* exhibited a similar range of colours. Colours as a food stimulant to *O. armatus* was therefore not considered in this study. In the green plant, chemicals which assist insects in their recognition of food plants are largely secondary plant chemicals which are often botanically restricted (HSIAO, 1969). On the other hand those which elicit feeding response are primary plant chemicals, including sugars, amino acids, lipids, steroids and certain vitamins. Although certain chemical constituents of a few yeasts and fungi are known, the relationship between chemicals and food selection by microphytophages is largely unknown. Substances eliciting feeding response amongst macrophytophagous insects are also components of microflora, and one or more of these components may elicit feeding in *O. armatus.* The low palatability of certain yeasts and fungi to *O. armatus* may similarly be associated with chemicals, either in the cell content, or in extracellular catabolites.

The selective grazing of a plant, as exemplified by *O. armatus* ingesting a preponderance of either spores or hyphae, is common amongst phytophagous insects, and can often be attributed to plant morphology (DETHIER, 1966). Among fungi, size and shape of spores and hyphae may influence their ingestion. For example large spores and long filamentous hyphae may be precluded from ingestion. The present study did not produce evidence of the importance of these morphological features as restricting ingestion. *O. armatus* ingested the long filamentous hyphae of *Absidia spinosa* in preference to its small spores. Similarly the relatively large conidia of *Alternaria tenuis* and *Epicoccum nigrum* were not precluded from ingestion, although they occured in the gut of *O. armatus* with less frequency than hyphae. The preference for spores from *Trichoderma viride* and hyphae from *Botrytus cinerea,* in multi-choice experiments with sporulating and non-sporulating forms of each species precludes selection of those components by *O. armatus* on the basis of any obvious morphological features, both have similar morphology. The cause of selective grazing by *O. armatus* is not obvious, although fungal attributes such as physiological state, chemical composition, and relative availability of components, e.g. hyphae and spores, may influence selection.

Interchanging the positions of the more preferred foods with those least preferred, did not affect the animal's food preference. It would therefore appear that in these experiments *O. armatus* was able to seek out a highly

preferred food. Observations of the feeding preferences of certain macrophytophagous insects (DETHIER, 1966) have shown that an individual's food preference may be modified by previous experience, such that an animal will choose the food upon which it has previously fed, thus demonstrating an aquired taste. In this study, *O. armatus* may demonstrate an acquired taste, since food positions were interchanged without significantly affecting the animal's food preference. There is, however, no evidence to indicate whether those animals feeding on a specific food, prior to the interchange of food positions, were the same animals which were later found on a food in its new position.

Food preferences exhibited by *O. armatus* under laboratory conditions may not necessarily parallel those in the field, for as stated by TRIBE (1950), food preference may be a function of plant and animal attributes under particular environmental conditions. For example, the chemical constituents and morphology of fungi and yeasts under cultivation, may differ from those in the field (COCHRANE, 1958; HEAL and FELTON, 1970). Similarly in the laboratory a sample of yeast or fungus may, through mechanical damage, become more or to less attractive to the animal. Nevertheless COLEMAN and MACFADYEN (1966), have shown that food preference displayed by certain Collembola (*Onychiurus procampatus* Gisin and *Folsomia quadrioculata* (Tullb.)) in the laboratory were similar to those observed under field conditions when the animals were confronted with a similar range of foods.

A horizontal layer of a soil profile shows considerable complexity of structure (ANDERSON, 1971) and may, as suggested by FREEMAN (1968), and MILLER (1969), contain a mosaic of microhabitats. The species of yeasts and fungi used in this study are common in beech, and may also ooccur in sweet chestnut woodland. However, the microhabitats of all these species of yeast and fungi may not necessarily concur with that of *O. armatus*. Therefore extrapolation of these laboratory food preference data to the field would, without further experiments, be imprudent. In the field, availability may determine which food is ultimately eaten. However, as shown by LEIGHTON and BOOLOOTIAN (1963), and CAREFOOT (1973), in studies of feeding amongst certain aquatic invertebrates, the most preferred food mat not necessarily be the most abundant food, nor may it provide the best nutritional value to the animal.

The apparent acceptability, to *O. armatus*, of all species of yeasts and fungi investigated in this study may indicate that the animal is able to obtain its nutritional requirements from a range of fungal species. This ability of *O. armatus* to apparently diversify its food source, would be of significance for the survival of the animal in times when certain food species may be unavailable.

It is evident that laboratory food preference experiments provide a useful form of investigation into the diet and feeding behaviour of Collembola.

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Summary

The fungal feeding habits of *Onychiurus armatus* (Collembola) were investigated under laboratory conditions using multi-choice food experiments. All 34 foods tested were ingested, but significant ($P < 0.05$ to $P < 0.001$) differences exist between the preference to *O. armatus* of these foods. The effects of fungal attributes such as physiological state, chemical composition and morphology in determining food preference is discussed.

References

Anderson (J. M.), 1971. — Observations on the vertical distribution of Oribatei (Acarina) in two woodland soils. In *Organismes du sol et production primaire.* IV. Colloquium pedobiologiae, Dijon, 1970, pp. 329-344, I.N.R.A. Publ. 71-7, Paris.

Anderson (J. M.) and Healey (I. N.), 1972. — Seasonal and inter-specific variation in major components of the gut contents of some woodland Collembola. *J. Anim. Ecol.*, **41**: 359-368.

Beck (S. D.), 1965. — Resistance of plants to insects. *A. Rev. Ent.*, **10**: 207-232.

Bödvarsson (H.), 1970. — Alimentary studies of seven common soil inhabiting Collembola of Southern Sweden. *Ent. scand.*, **1**: 74-80.

Caldwell (R.), 1963. — Observations on the fungal flora of decomposing beech litter in soil. *Trans. Br. mycol. Soc.*, **46**: 249-261.

Carefoot (T. H.), 1973. — Feeding, food preference, and the uptake of food energy by the supralittoral isopod *Ligia pallasii*. *Mar. Biol.*, **18**: 228-236.

Cochrane (V. W.), 1958. — *Physiology of Fungi*, Wiley, New York.

Coleman (D. C.) and Macfadyen (A.), 1966. — The recolonisation of gamma-irradiated soil by small arthropods. *Oikos*, **17**: 62-70.

Dethier (V. G.), 1966. — Feeding behaviour. In *Insect Behaviour* (P.T. Haskell, Ed.), pp. 46-58, Symp. R. ent. Soc. Lond. 3, Bartholomew Press, Dorking.

Fraenkel (G.), 1959. — The raison d'etre of secondary plant substances. *Science, N. Y.*, **129**: 1466-1470.

Freeman (B. E.), 1968. — Studies on the ecology of adult Tipulidae (Diptera) in southern England. *J. Anim. Ecol.*, **37**: 339-362.

Gilmore (S. K.) and Raffensperger (E. M.), 1970. — Foods ingested by *Tomocerus* spp. (Collembola, Entomobryidae) in relation to habitat. *Pedobiologia*, **10:** 135-140.

Goto (H.), 1961. — Simple technique for the rearing of Collembola and a note on the use of a fungistatic substance in the cultures. *Entomologist's mon. Mag.*, **96**: 138-40.

Heal (O. W.) and Felton (M. K.), 1970. — Soil Amoebae: their food and their reaction to microflora exudates. In *Animal Populations in Relation to their Food Resources* (A. Watson, Ed.), pp. 145-162, British Ecological Society Symposium No. 10, Blackwell Scientific Publications, Oxford.

HOGG (B. M.) and HUDSON (H. J.), 1966. — Micro-fungi on leaves of *Fagus sylvatica*. 1. *The micro-fungal sucession. Trans. Br. mycol. Soc.*, **49**: 185-192.

HSIAO (T. H.), 1969. — Adenine and related substances as potent feeding stimulants for the Alfalfa weevil, *Hypera postica. J. Insect. Physiol.*, **15**: 1785-1790.

JENSEN (V.), 1963 a. — Studies on the microflora of Danish beech forest soils. IV. Yeasts and yeast-like fungi. *Zbl. Bakt. II.*, **117**: 41-65.

JENSEN (V.), 1963 b. — Studies on the microflora of Danish beech forest soils. V. The microfungi. *Zbl. Bakt. II*, **117**: 167-179.

JENSEN (V.), 1964. — On the occurrence of yeasts in forest soils. In *Transactions of the Eighth International Congress of Soil Science*, Bucharest, Vol. III, pp. 561-567.

KNIGHT (C. B.) and ANGEL (R. A.), 1967. — A preliminary study of the dietary requirements of *Tomocerus* (Collembola). *Am. Midl. Nat.*, **77**: 510-517.

KUBIENA (W. L.), 1955. — Animal activity in soils as a decisive factor in establishment of humus forms. In *Soil Zoology* (D. K. McE. Kevan, Ed.), pp. 73-82, Butterworths Scientific Publications, London.

LEIGHTON (D. L.) and BOOLOOTIAN (R. A.), 1963. — Diet and growth in the black abalone *Haliotis cracherodii. Ecology*, **44**: 227-238.

MCMILLAN (J. H.), 1975. — Interspecific and seasonal analyses of the gut contents of certain Collembola (Family Onychiuridae). *Rev. Ecol. Biol. Sol*, **12**: 449-451.

MCMILLAN (J. H.) and HEALEY (I. N.), 1971. — A quantitavie technique for the analysis of the gut contents of Collembola. *Rev. Ecol. Biol. Sol*, **8**: 295-300.

MACNAMARA (C.), 1924. — The food of Collembola. *Can. Ent.*, **56**: 99-105.

MILLER (R. S.), 1969. — Competition and species diversity. *Brookhaven Symp. Biol.*, **22**: 63-70.

POOLE (T. B.), 1959. — Studies on the food of Collembola in a Douglas fir plantation. *Proc. Zool. Soc. Lond.*, **132**: 71-82.

SCHALLER (F.), 1950. — Biologische beobachtungen an humusbildenden bodentieren, insbesondere an collembolen. *Zool. Jb.*, **78**: 506-525.

SINGH (S. B.), 1969. — Preliminary observations on the food preference of certain Collembola (Insecta). *Rev. Ecol. Biol. Sol*, **6**: 461-467.

STREBEL (O.), 1932. — Beiträge zur ökologie, und physiologie einheimischer collembolen. *Z. Morph. Ökol. Tiere*, **25**: 31-153.

THORSTEINSON (A. J.), 1960. — Host selection in phytophagous insects. *A. Rev. Ent.*, **5**: 193-208.

TÖRNE (E. von), 1967 a. — Beispiele für indirekte einflüsse von bodentieren auf die rotte von zellulose. *Pedobiologia*, **7**: 220-227.

TÖRNE (E. von), 1967 b. — Beispiele für mikrobiologene einflüsse auf den massenwechsel von bodentieren. *Pedobiologia*, **7**: 296-305.

TRIBE (D. E.), 1950. — The behaviour of the grazing animal - a critical review of present knowledge. *J. Br. Grassld Soc.*, **5**: 209-214.